MODE OF LIFE AND AUTECOLOGY OF SILURIAN-DEVONIAN GRAMMYSIIDAE (BIVALVIA)

by L. F. MARSH

ABSTRACT. The Grammysiidae are a Palaeozoic family of mainly infaunal anomalodesmatan Bivalvia that lived in very shallow marine environments. Since they were edentulous, the problem of shearing of the valves during burrowing was overcome by the cincture (radial furrows and ribs), which folded the ventral margin. This folded venter provided an active saw during burrowing. Species that burrowed in very high-energy environments showed very marked ventral folding, strong concentric ribs on the anterior end, a fairly large anterior end, and usually a disc-shaped, not highly inequilateral, shell of low inflation. Byssally attached forms reduced the anterior end, expanded the posterior end, had a less folded venter, more elongate shell, lost the strong anterior concentric ribbing, and were more inflated. Shell form and ornamentation is related to the environment and mode of life.

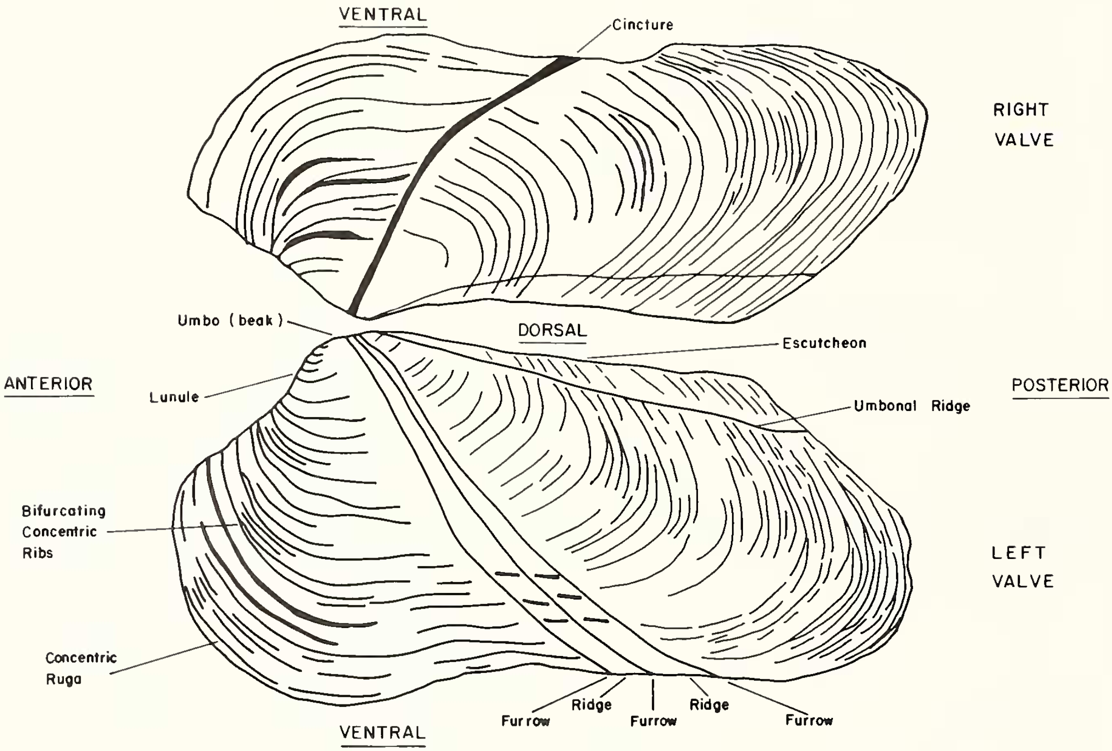
BIVALVES of the Palaeozoic family Grammysiidae (largely Silurian and Devonian) belong to the subclass Anomalodesmata and, like most forms in this subclass, lack dentition. The main external morphological features of the family are shown in text-fig. 1. The most important characteristic is the radial cincture, composed of ribs and/or furrows which pass from the umbones to the ventral margin. The only inequality in the valves is in the form of the cincture. This differs in the two valves so that a rib on one valve alternates with a furrow on the other to cause the ventral margin to be folded (Pl. 60, fig. 3). The function of this is discussed further below. Most Grammysiidae also possess concentric, bifurcating ribs (text-fig. 1), a lunule, and an escutcheon. By comparison with modern bivalves (and particularly the work on modern bivalves by Stanley 1970), it is possible to ascertain the functional significance of the shell morphology in the Palaeozoic Grammysiidae.

MORPHOLOGY AND MODE OF LIFE

Since all species of the Grammysiidae show the greatest inflation in the dorsal to central part of the shell, they must all have been, at least partly, infaunal. The relationship between position of maximum inflation and mode of life in modern bivalves is shown by Stanley (1970, p. 27 and fig. 8). The Grammysiidae must also have lived close to the sediment surface, in permanent contact with the sediment-water interface, since none of them possessed a pallial sinus. Many species of Grammysiidae lived in the littoral zone and all species lived in very shallow water. Interpretation of the life environments are readily confirmed by sedimentary structures and lithologies as recorded, for example, by Potter and Price (1965) and Potter (1967, p. 280). Some species, however, lived in lower energy environments (Holland and Lawson 1963) and were not frequently exhumed. Consequently they appear to be more streamlined for permanent infaunal life. The morphology of some species indicates that they became infaunally or semi-infaunally byssally attached. All members of the Grammysiidae lack dentition. This would have presented problems to an active burrowing bivalve, since the valves would have sheared over each other during burrowing if some assistance to burrowing was not available. I consider that this lack of dentition, associated in most cases with active burrowing, led to the development of the radial and concentric ornament in most of the species. The radial cincture (ribs and furrows) combined with concentric ribbing would have provided an active sawing mechanism to aid rapid, repeated burrowing. Stanley (1970, p. 64) recognized the importance of the function of this type of ornament in modern bivalves. It is of note that the species

[Palaeontology, Vol. 27, Part 4, 1984, pp. 679-691, pls. 60-61.]

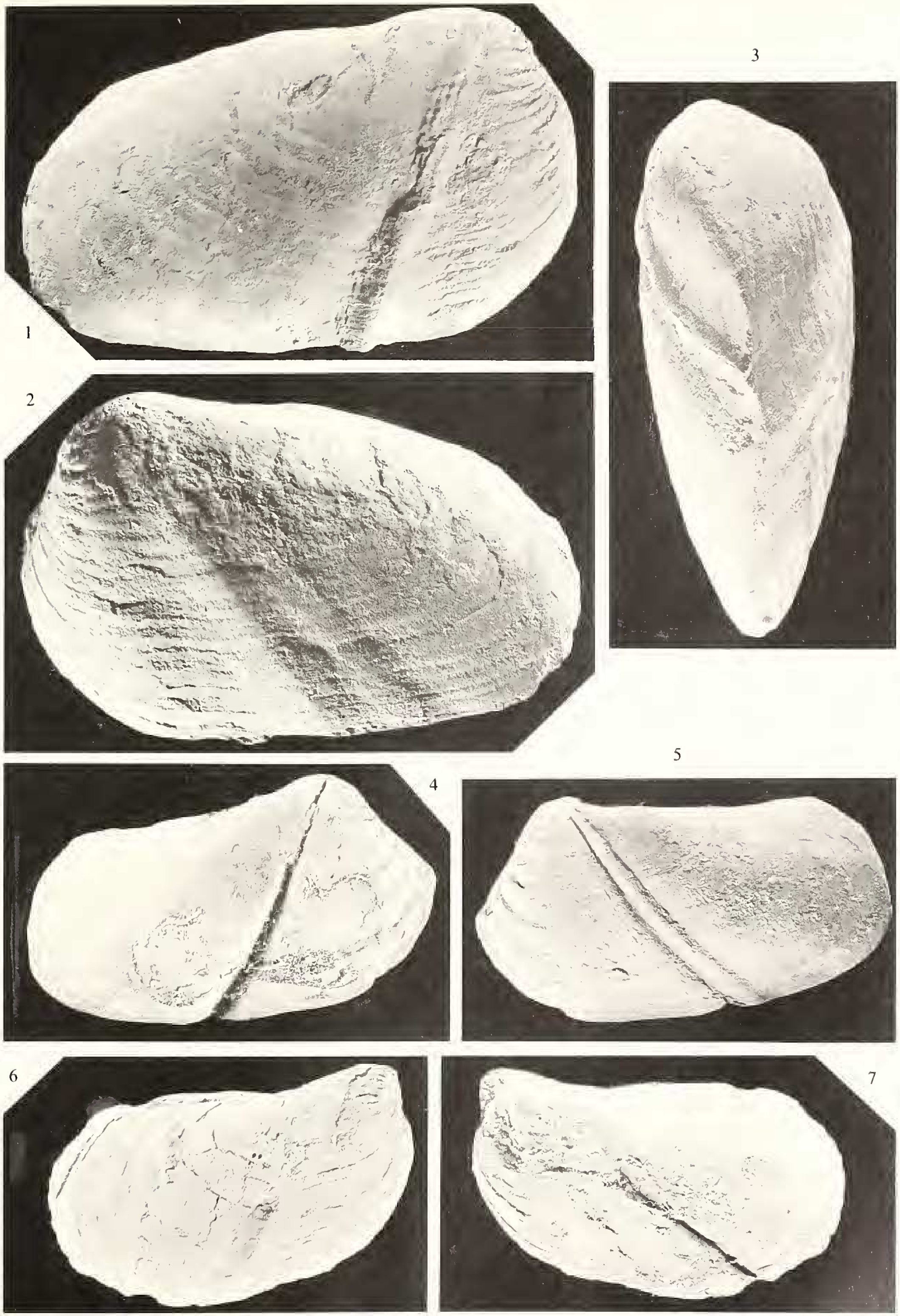
that lived in the higher energy conditions, and hence were more likely to be exhumed frequently, have better developed ornament, e.g. *Grammysia triangulata* (Salter) (Pl. 61, fig. 1; text-fig. 3*k*) and *G. grammysioides* (Salter) (Pl. 61, fig. 2; text-fig. 3*p*). The latter species also shows marked bifurcation of the concentric ribbing as an additional burrowing tool, as do *G.* sp. nov. *d.* (Marsh 1976, pp. 359–363, pl. 14, figs. 1–9; pls. 15–18; pl. 19, figs. 1–9) (herein Pl. 60, figs. 4, 5; text-fig. 3*d*) and *G. cingulata* (Hisinger) (Pl. 60, figs. 1–3; text-fig. 3*c*). The cincture alone folded the venter (Pl. 60, fig. 3) and would have provided a sawing mechanism. Most of the species of this family can be shown to have had a strong ligament to help prevent shearing of the valves, which would have occurred owing to the lack of dentition. Scars made by ligament attachment along the hinge line have been illustrated by Bambach (1971, p. 180, fig. 10).



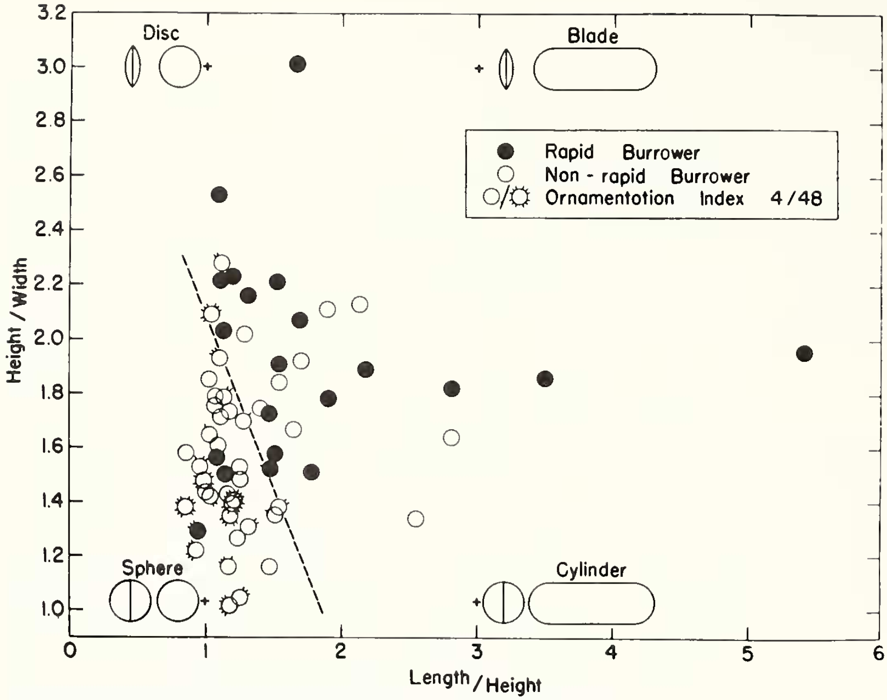
TEXT-FIG. 1. Main morphological features of Grammysiidae.

EXPLANATION OF PLATE 60

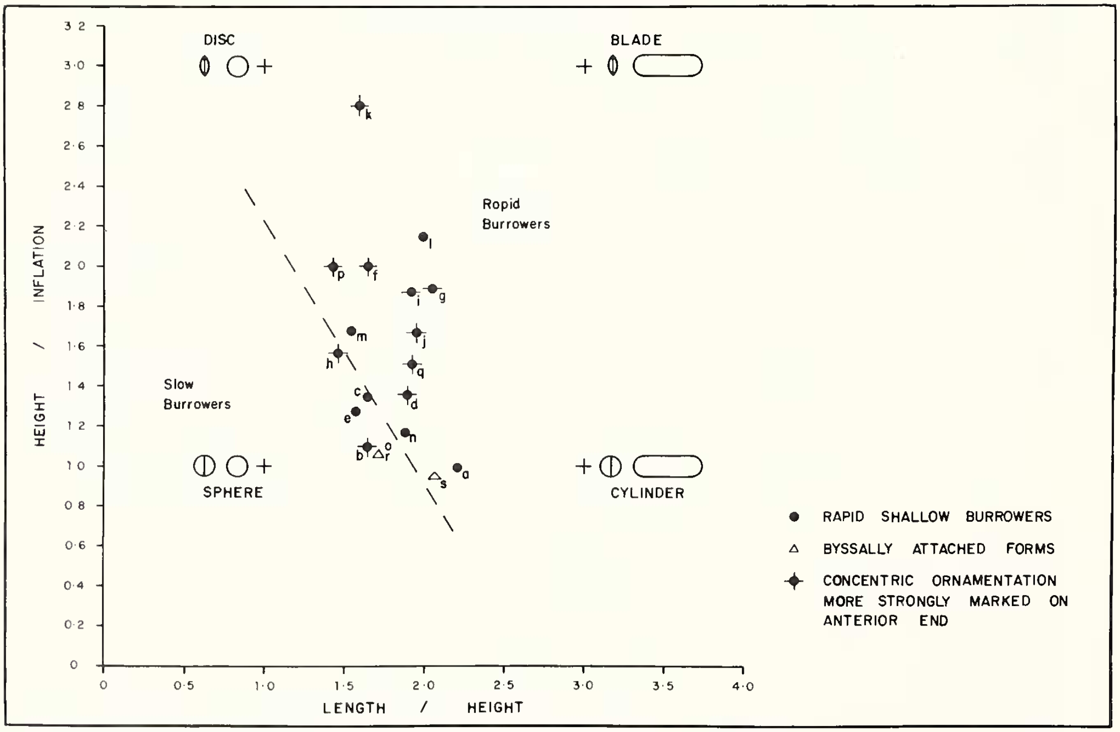
Figs. 1–5 = ancestral grammysiid species. Figs. 1–3, *Grammysia cingulata*, Much Wenlock Limestone, Formation, Dudley, BM L49130, right valve, left valve, and ventral view showing folding produced by the alternation of ribs and furrows of the cincture in each valve. Figs. 4, 5, *G.* sp. nov. *d*, Much Wenlock Limestone Formation, Dudley, BU 276, 294, right and left valves. Figs. 6, 7, *G.* sp. nov. *o*, Wenlock sandstone, Bryn Craig, Usk inlier, IGS 24217, right and left valves. All ×2.



MARSH, Silurian *Grammysia*



TEXT-FIG. 2. Relation of burrowing rate to gross shell shape and shell ornamentation in recent bivalves (from Stanley 1970, fig. 25).



TEXT-FIG. 3. Relation of inferred burrowing rate to gross shell shape and shell ornamentation in Grammysiidae.

The shapes of the shells of Grammysiidae vary considerably. The shape of a particular species is a reflection of its mode of life and adaptation of the animal to its environment, as produced by natural selection. A change in the environment and, therefore, in the mode of life of a species resulted in a change in morphological features such as the shell form. Species evolved owing to selection pressure produced by environmental changes. In areas where environmental changes occurred speciation was much more rapid than in areas where environmental conditions were stable (Raup and Stanley 1971, p. 99). Bretsky (1973, p. 2090) recognized this in stating that '. . . the degree of morphological distinctiveness at any one time in the fossil record for a particular clearly defined ecological grouping probably reflects . . . the degree of difference between local environmental settings'. A particular species of grammysiid thus survived in one area where the environment did not change and yet was replaced by different species in an area where the environment did change. Stratigraphical ranges of any one species thus vary considerably from place to place, being dependent on the environment. Grammysiid bivalves are therefore very good environmental indicators. It is common to find morphologically similar bivalves developed at different horizons owing to convergent evolution in unrelated species living in similar environments.

From the generalized, straight-hinged ancestors *G. cingulata* and *G.* sp. nov. *d.*, differently shaped species evolved as adaptations to different environmental conditions. Disc- and triangular-shaped forms, with concentric ribs much more strongly marked on the anterior end, evolved to cope with very high energy conditions and frequent exhumations. Other forms became byssally attached, lived in rather lower energy conditions and developed more elongated shells, and reduced the anterior end.

The relationship of shell form to mode of life in living bivalves was shown by Stanley (1970, p. 60, fig. 25) (herein text-fig. 2). Compare text-fig. 3 for the Palaeozoic Grammysiidae, which shows the positions of the type specimens of each of the grammysiid species. The more rapid burrowers have a high height/inflation ratio and high length/height ratio. They are therefore either disc- or blade-shaped shells. Concentric ornamentation more strongly marked on the anterior end also appears to assist burrowing speed. If, however, the shell shape itself allows extremely rapid burrowing, then the additional concentric ornament appears to be unnecessary, e.g. plot 1 of *G. extrasulcata* (Salter), an elongate shell with very low inflation.

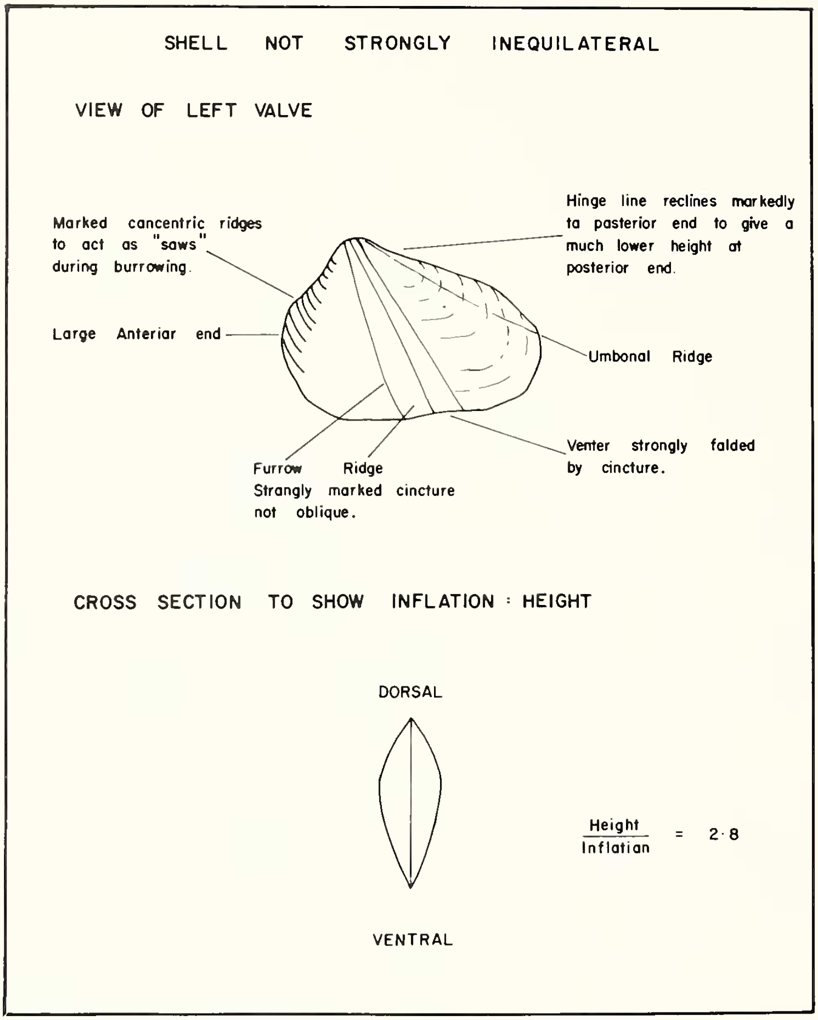
From detailed biometric studies of Silurian–Devonian Grammysiidae, two groups which exhibit distinctive morphological features have been recognized. These are interpreted as follows:

Group (i). Rapid, shallow burrowers (text-fig. 4).
Group (ii). Semi-infaunal, byssally attached species (text-fig. 5).

Group (i)

The shallow-burrowing Grammysiidae living in very high energy environments (where exhumation from the sediment during life is commonplace and, therefore, the ability to carry out rapid, repeated burrowing throughout life is a necessity) show a combination of the following morphological features (text-fig. 4):

(*a*) A shell that is not highly inequilateral, to aid ease of rocking from side to side during burrowing.
(*b*) A shell shape that is discoidal or triangular, or very elongate and of very low inflation.
(*c*) A hinge line that is either strongly reclining towards the venter or parallel to the venter, not divergent (text-fig. 6, e.g. *G. triangulata*).
(*d*) The greatest height of the shell at the umbones.
(*e*) Low inflation.
(*f*) High height/inflation ratio.
(*g*) A large anterior end, to allow ease of penetration into the sediment as burrowing was initiated (text-fig. 7), e.g. *G. triangulata* to contrast with the byssally attached *G. obliqua*.
(*h*) An anterior end furnished with strong concentric ridges (for sawing) that are either absent or are only very weakly marked on the rest of the shell.
(*i*) A well-developed, strongly marked cincture that causes a very marked folding of the entire venter, to act as a sawing mechanism.
(*j*) The valves usually found disarticulated and frequently broken.

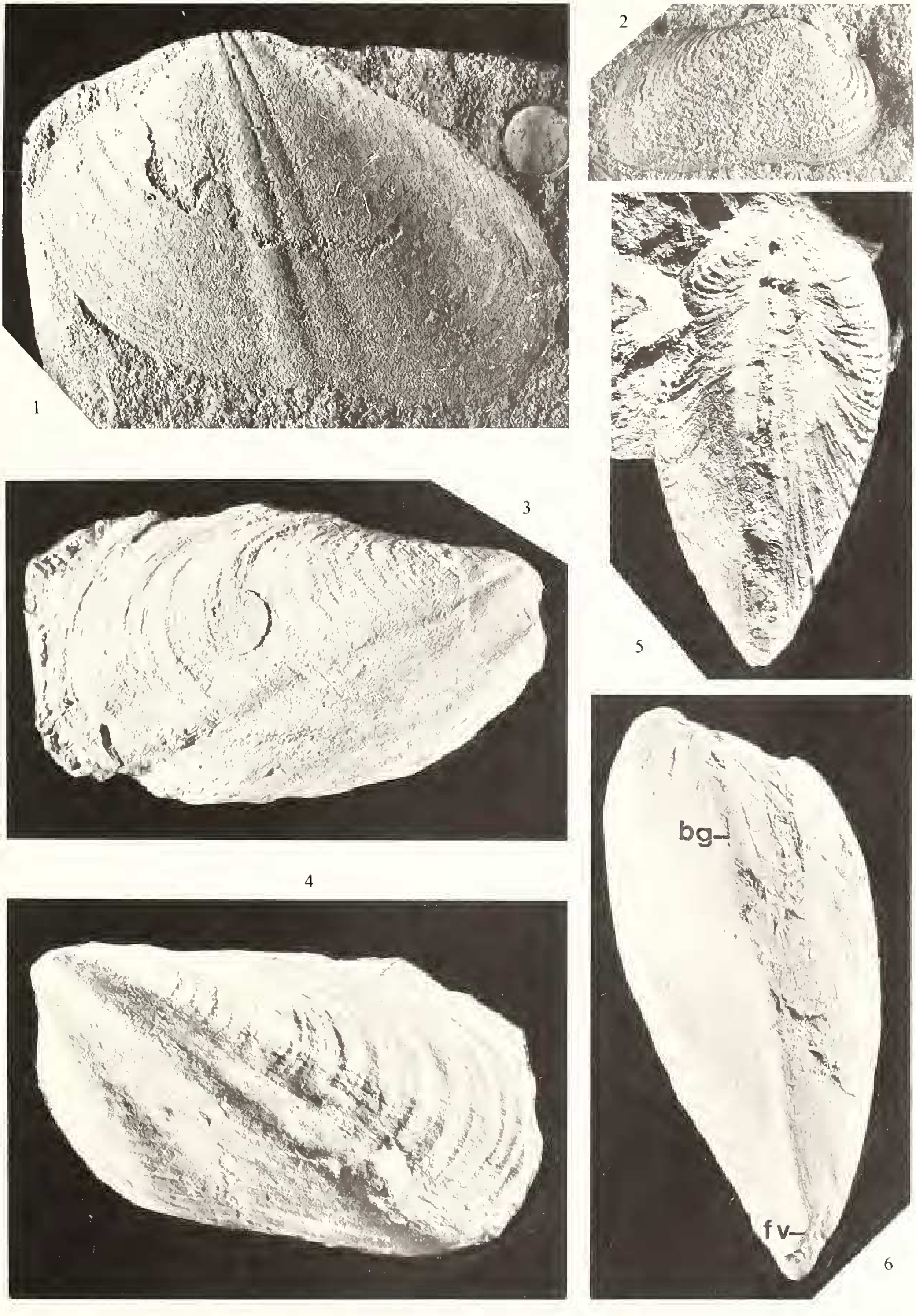


TEXT-FIG. 4. Typical morphological features of the shell developed in rapid, shallow burrowing Grammysiidae, e.g. *Grammysia triangulata*.

EXPLANATION OF PLATE 61

Fig. 1, *Grammysia triangulata*, Whitcliffian, Kirkby Moor Flags, Benson Knot, Kendal, Cumbria, a rapid burrower in very high energy conditions, IGS 12487, left valve. Fig. 2, *G. grammysioides*, derived fossil in Triassic Budleigh Salterton Pebble Bed, SE Devon, specimen derived from Lower Siegenian, Devonian of Brittany, BM L15, 821, a right valve, another rapid burrower.

Figs. 3–6, *G. obliqua*, Ludlow, Usk inlier, a byssally attached species showing oblique cincture, very small anterior end, and greatest height of shell at posterior end. Fig. 3, IGS 12468, holotype, right valve. Fig. 4, NMW G482, left valve. Fig. 5, IGS G Sb 4225, dorsal view, showing dorso-posterior gape and scars of attachment of the strong external ligament along the escutcheon. Fig. 6, BM L 5438 (a) antero-ventral view, with anterior end uppermost, showing narrow antero-ventral byssal gape (bg) and folded venter (fv) near posterior end, produced by the alternation of the cincture in each valve. All ×2.

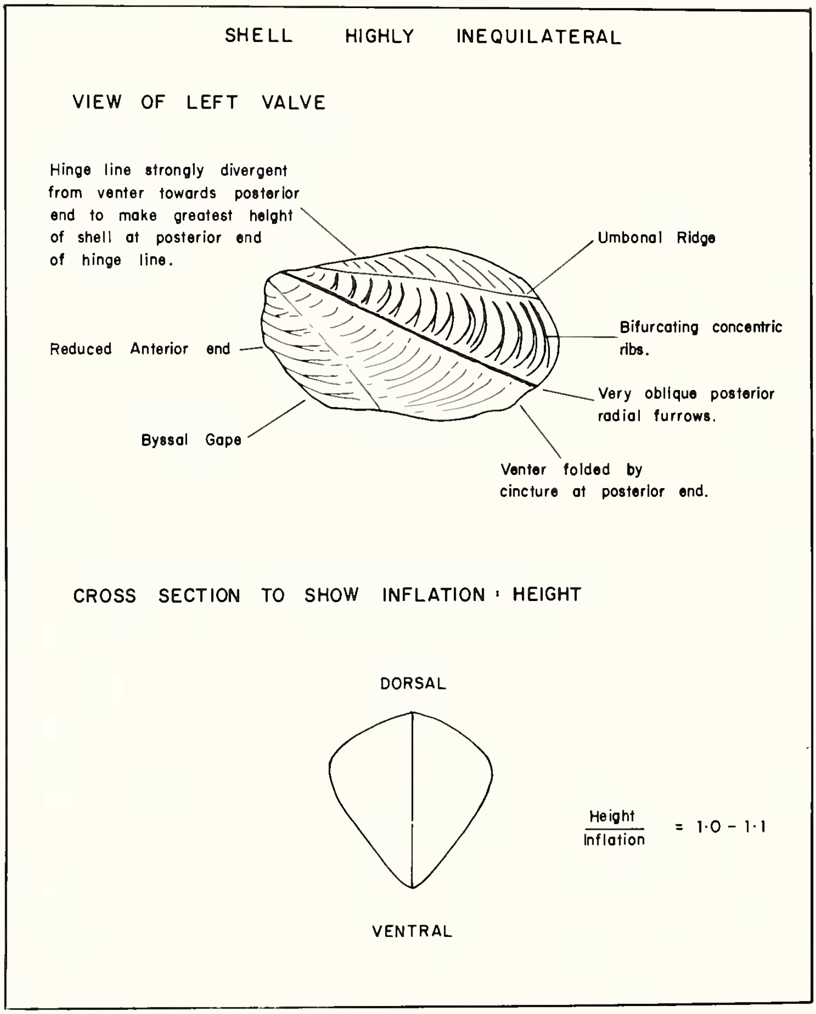


MARSH, Silurian *Grammysia*

Group (ii)

Byssally attached infaunal or semi-infaunal Grammysiidae show a combination of the following morphological features (text-fig. 5):

(*a*) An elongate shell.
(*b*) A highly inequilateral shell.
(*c*) A hinge line that is strongly divergent from the venter towards the posterior end (text-fig. 6, e.g. *G. obliqua*).
(*d*) The greatest height of the shell at the posterior end of the hinge line.
(*e*) High inflation.
(*f*) Low height/inflation ratio.



TEXT-FIG. 5. Typical morphological features of the shell developed in semi-infaunal byssally attached Grammysiidae, e.g. *Grammysia obliqua*.

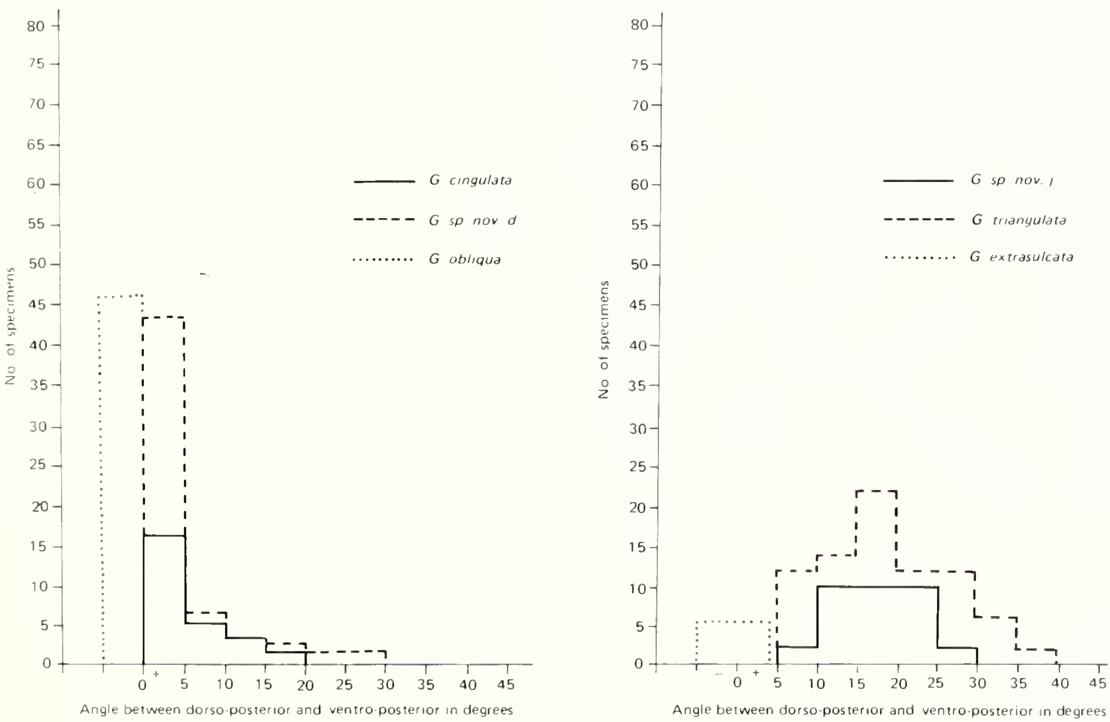
(*g*) A greatly reduced anterior end (text-fig. 7, e.g. *G. obliqua*).
(*h*) The small anterior end marked with fine concentric ridges that are not better marked on the anterior end than they are on the rest of the shell.
(*i*) A reduced, very obliquely marked cincture composed only of furrows, which causes a folding only of the extreme posterior end of the venter.
(*j*) An expanded posterior end.
(*k*) An anterior-ventral byssal gape.
(*l*) The valves usually found closed and articulated.

G. obliqua McCoy illustrates all the above features (Pl. 61, figs. 3–6).

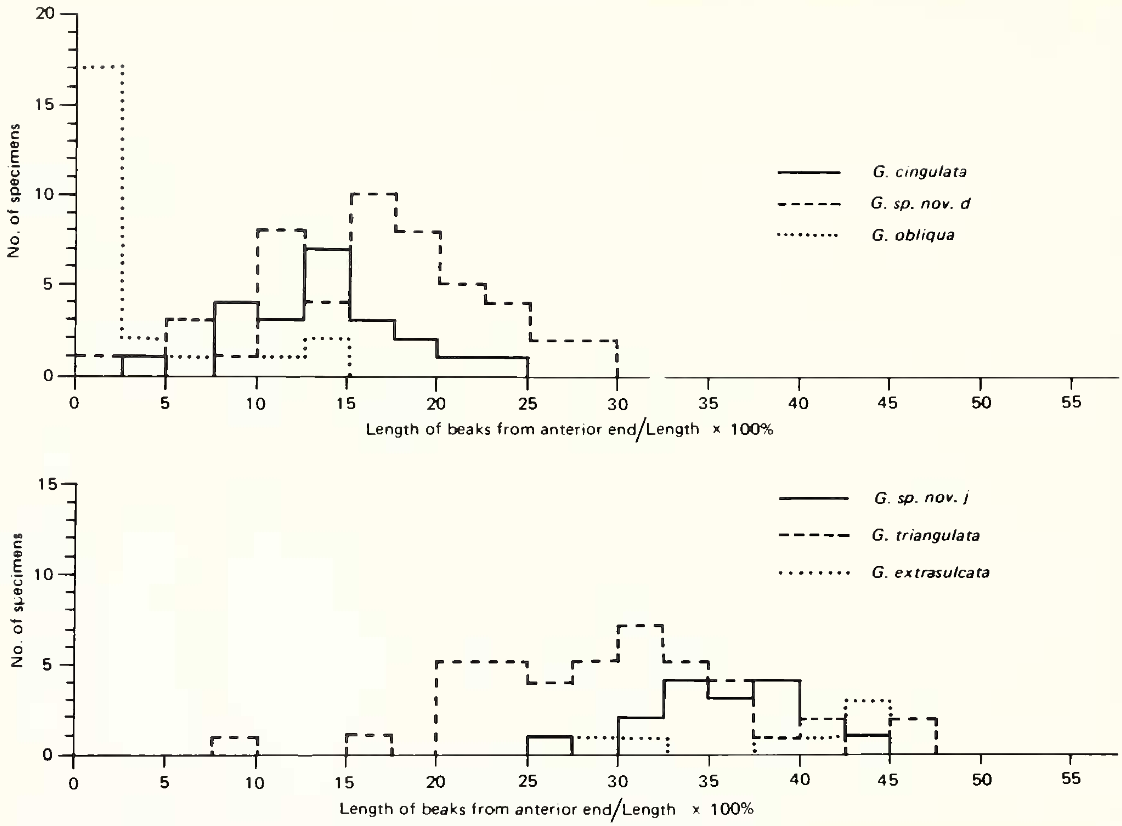
SPECIAL ADAPTATIONS

Some specialized adaptive morphology has been noticed in certain species. The byssally attached *G. obliqua* (text-fig. 3*r*) evolved from *G. cingulata* (text-fig. 3*c*), a moderately active shallow burrower, via a new species *G.* sp. nov. *o.* (text-fig. 3*o*) (Marsh 1976, pp. 405–411, pls. 34–36; herein Pl. 60, figs. 6, 7) which became byssally attached. From text-fig. 3 it can be seen that both the byssally attached species are much more inflated than active burrowing species like *G. triangulata* (*k*). Even *G. cingulata* (*c*), the ancestral species, would have had only a modest burrowing speed as indicated by its plot on the graph in text-fig. 3.

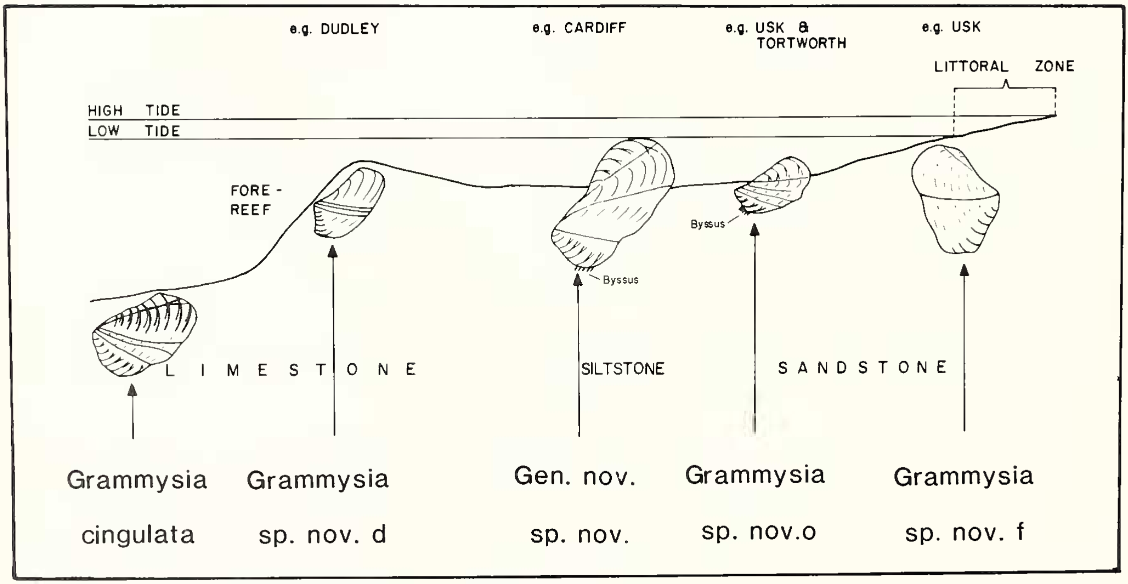
G. sp. nov. *o.* (text-fig. 8) shows certain changes in its morphology (compared with *G. cingulata*) concurrent with the acquisition of an adult byssus. The anterior end is reduced and the cincture is more oblique. Certain of the ancestral features, however, remain, e.g. the straight hinge line.



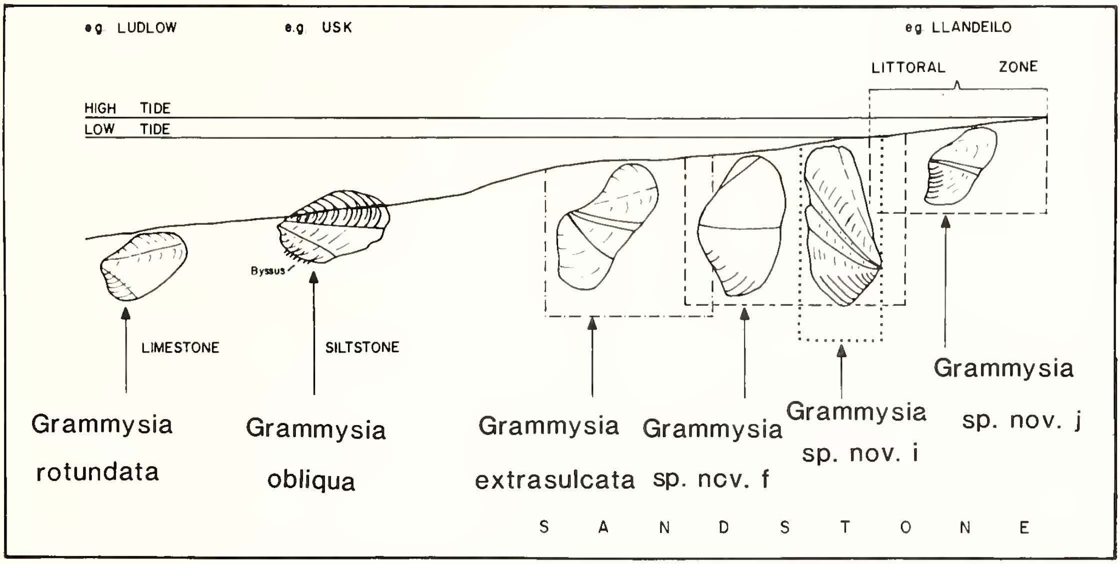
TEXT-FIG. 6. The angle in degrees between dorso-posterior and ventro-posterior in six grammysiid species.



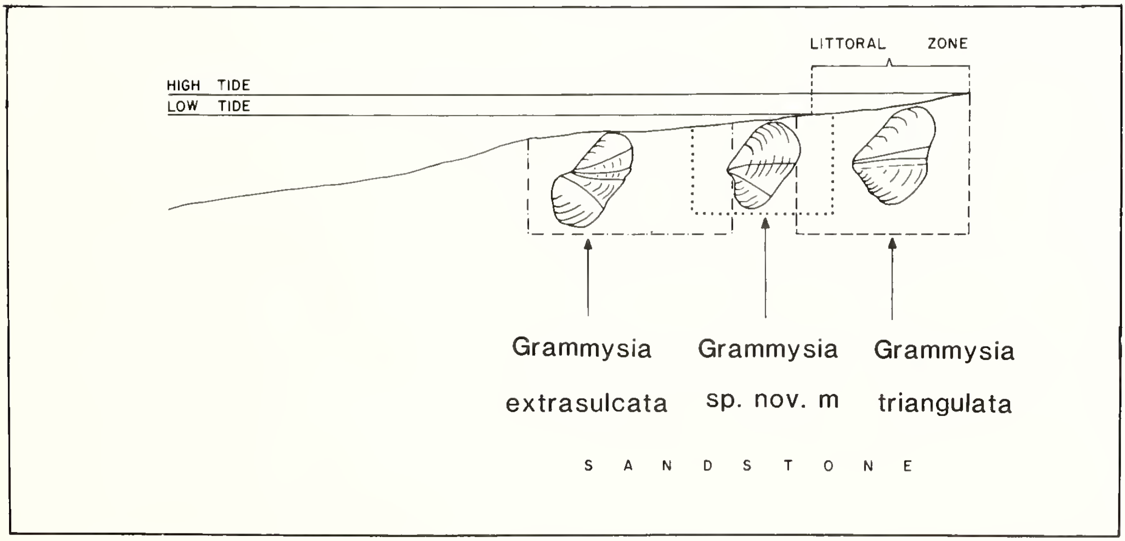
TEXT-FIG. 7. The length of the beaks from the anterior end as a percentage of the total length in six grammysiid species.



TEXT-FIG. 8. Grammysiid life position and environmental zonation in the upper Wenlock (Homerian).



TEXT-FIG. 9. Grammysiid life position and environmental zonation in the Ludlow (upper Bringewoodian).



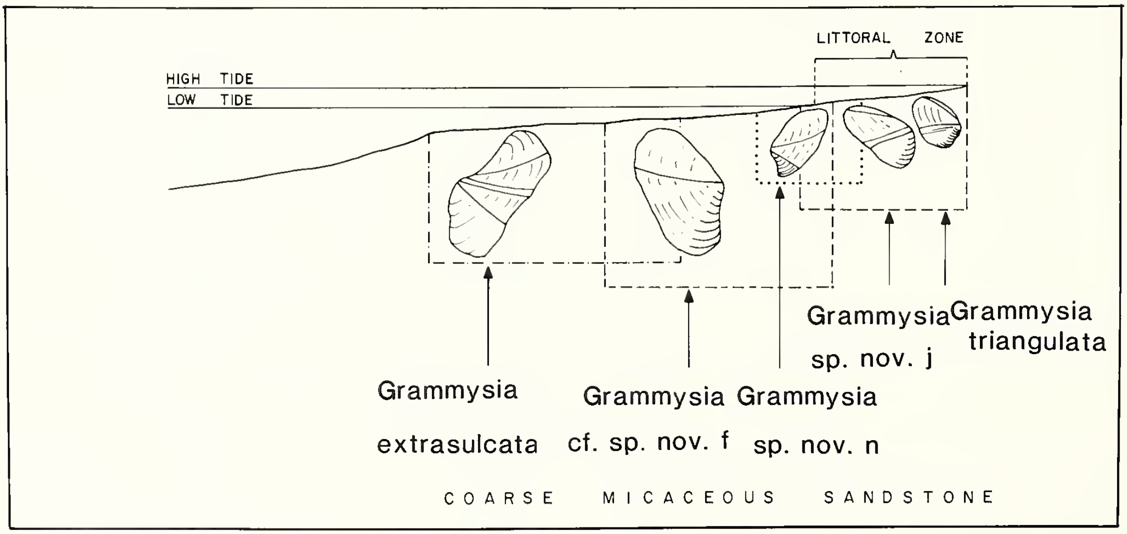
TEXT-FIG. 10. Grammysiid life position and environmental zonation in the Ludlow (Whitcliffian) of the Lake District, England

The umbonal ridge (text-fig. 8) running from the umbo to the postero-ventral angle marks off a much less-inflated dorso-posterior slope to the shell. I believe that the dorso-posterior slope would have been above the sediment in life position and that the umbonal ridge marked the sediment-water interface. I do not believe that the posterior furrow of the cincture marked the sediment-water interface, nor that the whole of the posterior end of the shell protruded from the sediment as Bambach (1971, p. 175, fig. 9) suggested for '*G. obliqua*' (although the species he discussed was the very similar, but more highly evolved species *G. acadica* Billings). The two posterior furrows of the cincture are not in the same position on the two valves and, therefore, if the posterior furrows did represent the sediment-water interface, then this interface would have been at different levels on the two sides of the specimen. The umbonal ridge therefore probably represents the sediment-water interface in life and only the extreme dorsal posterior end protruded from the sediment. It is, however, certainly possible that from time to time some of the sediment was removed from above the bivalve by current, tidal, and wave action, and indeed the nature of the sediments suggest this.

With the frequent inwashes of sediment that occurred, *G.* sp. nov. *o* must have been able to retain contact with the sediment surface. It seems likely that it did this by changing the angle at which it lived relative to the sediment-water interface. As suggested by Bambach (1971, p. 178) for '*G. obliqua*', *G.* sp. nov. *o* probably normally lived at an angle of about 40° to the sediment-water interface. If it was inundated with sediment, I believe that it could have increased this angle by action of the foot and use of the cincture and concentric ridges, to maintain contact between the siphons and the sediment-water interface (text-fig. 8). It could have done this without damage to the byssus (Marsh 1976, p. 410, fig. 67). Certainly in the high-energy environment in which it lived, *G.* sp. nov. *o* must have been able to cope with small influxes of sediment that would have occurred from time to time. At other times erosion took place and this species then returned to its more normal life position. The shell of *G.* sp. nov. *o* therefore shows special adaptation to a semi-infaunal byssally attached mode of life in an environment of moderately high energy.

The descendent species *G. obliqua* probably retained a cincture to pull itself down into the sediment from time to time to avoid exhumation (Marsh 1976, pp. 421, 422) and to avoid complete inundation when moderate rates of sedimentation occurred, in a similar way to *G.* sp. nov. *o*.

General life positions are illustrated in text-figs. 8–11.



TEXT-FIG. 11. Grammysiid life position and environmental zonation in the topmost lower Downton of South Central Wales.

Acknowledgements. I acknowledge the receipt of an ILEA Research Assistantship, during the tenure of which much of the research for this paper was carried out. Thanks are expressed to Miss J. E. Bruch (Exploratory Division, British Gas) for production of the originals of some of the figures. I also thank Dr. J. F. Potter (Farnborough College of Technology) and my husband, Dr. R. C. Marsh (South London College) for critically reading the manuscript. This paper formed a contribution to the Symposium on Autecology of Silurian Organisms at Glasgow, September 1983 (IGCP Project 53—Ecostratigraphy). Specimens are housed in the British Museum (Natural History), London (BM), Institute of Geological Sciences, London (IGS), Birmingham University (BU), and the National Museum of Wales, Cardiff (NMW).

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Manuscript received 21 May 1983
Revised manuscript received 22 January 1984